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Additional Social and Physiological Aspects of Respiratory Behavior in Small Tarpon.

Arthur Shlaifer

New York Aquarium & U. S. Fish & Wildlife Service, Woods Hole, Mass.

Introduction.

Tarpon, *Tarpon atlanticus* (Cuv. & Val.), whose swimbladders contain considerable alveolar tissue, periodically rise to the surface to breathe atmospheric oxygen despite their extensive gill surfaces and the relatively high oxygen content of the waters they normally inhabit.

The work reported here represents a continuation of the program of investigation with small tarpon begun by Shlaifer & Breder (1940). In this earlier work, which, incidentally, is the first experimental report on this fish, it was found, among other things, that the surface rise of a tarpon to gulp air may induce similar rises in others in a group. For instance, in a group of four in a 50-liter aquarium, in 70% of the cases a rise by one tarpon would induce a rise in one or more companions. It was shown that "coincidence" was not involved as a disturbing factor and that, apparently, a tarpon had to be in a "physiologically receptive" state by virtue of a depleted oxygen supply before such imitative rises could be induced. In preliminary experiments, some success was attained in inducing rises by means of a silver-painted carved wooden tarpon model manipulated so as to simulate the normal rise of this fish. In the present report "model" experiments were considerably extended.

Shlaifer & Breder (1940) found that while the locomotor activity of tarpon did not change when the oxygen content of the water was raised from 2.50 cc. per liter to 5.60 cc., the rate of surface (respiratory) rises to gulp air decreased markedly. As a continuation of this line of investigation, experiments were performed to determine the effect of waters of distinctly low oxygen content on locomotor activity and surface rises; also, survival time was determined for tarpon whose access to the surface and hence to atmospheric oxygen was cut off.

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The Induction of Imitative Respiratory Rises.

As discussed above, it has been found (Shlaifer & Breder, 1940) that imitative surface rises in small tarpon may be induced by a manipulated wooden model as well as by other tarpon. Models have been used with and without success in various lines of investigation on behavior in fishes. Thus, Lissmann (1932) found that the characteristic fighting reaction of the Siamese fighting fish, *Betta splendens*, is elicited by plasticine models or paintings of the fish. Noble (1934) working with the dwarf sunfish, *Eupomotis gibbosus*, and Breder (1936) with the sunfish, *Lepomis auritus*, found that males would attempt to mate with a variety of objects irrespective of their general appearance provided they were manipulated so as to resemble somewhat the actions of a female ready to spawn. On the other hand, Spooner (1931) found that the bass, *Morone labrax*, was not attracted by various rough models of itself. Breder & Coates (1935), investigating the sex recognition of the guppy, *Lebistes reticulatus*, found that no reaction was given to carefully made models of female *Lebistes* with or without movement. Finally, Shlaifer (1940) failed to obtain a reaction to sunfish models by goldfishes.

Granted that a properly manipulated wooden model may induce imitative rises in tarpon, will other objects properly manipulated but differing appreciably from a tarpon in shape and color also induce rises and if so to what extent? Will a tarpon model or other objects be effective if manipulated so as to rise in a manner appreciably different from the normal one? In an attempt to answer these questions the experiments described below were performed.

Materials and methods. The animals used in these and other experiments described in this paper were 10–12 cm., presumably young, specimens sent from the collection at the New York

Aquarium but originally obtained along the Florida coast. They were kept in sea water and were fed chopped herring three times a week. The experimental group in the model tests was composed of six tarpon placed in 40 liters of standing sea water in a 48-liter rectangular assembled aquarium with transparent glass sides, whose dimensions were 55 cm. by 35 cm. and 25 cm. deep. The water temperature range was 19–22 degrees C. and the average oxygen content was 2.50 cc. per liter.

Four different types of object, all 10 cm. in length, were used as "models" in the attempts to induce imitative rises in the experimental animals. These were: 1. A silver-painted carved wooden model of a tarpon having no fins or mouth but possessing an "eye" fashioned out of a thumbtack. 2. A white spatula. 3. A piece of red rubber tubing 1 cm. in diameter. 4. A solid glass rod 4 mm. in diameter. Two pieces of string were attached to these objects at opposite ends. The object to be tested was suspended horizontally in the experimental aquarium containing the six tarpon, next to the long side of the aquarium nearest the observer, at a distance of 3.5 cm. from the bottom, the level at which the tarpon in that situation generally swam. The observer, seated about two feet away from the aquarium and facing one long side, manipulated the object by means of the two strings. The normal air-gulping rise of a tarpon is a rapid movement lasting a little less than a second from the start of the rise to the return to the normal position. Usually the animal rises to the surface almost vertically. In A of Table I this type of rise was simulated by properly manipulating the objects. In B of Table I the object or model was manipulated so as to produce a distinctly "abnormal" rise. The object was raised to the surface parallel with it rather than at a right angle and the rise from beginning to end lasted two seconds. The data in Table I are listed in terms of successful attempts to induce rises in the tarpon by means of the manipulated objects. Each time the object is raised to the surface is considered an "attempt." The attempt is considered successful if within one second or less following the start of the rise of the model one or more tarpon rise to the surface. Rises by the fishes two or three seconds after the object had risen might also have been imitative delayed reactions but were not considered. Indeed, such rises very rarely occurred. Either the fish would respond immediately or it would not rise for a minute or more. No effort was made to differentiate between induced imitative rises that involved varying numbers of tarpon. In fact, such differentiation is very difficult if not impossible since, except in rare cases in which two or more individuals arose at exactly the same time, one cannot determine whether the rise of the tarpon following very closely that of the first animal to rise is a response to the object or to the first tarpon.

Observations were made within a ten-minute experimental period. Every second, fourth, sixth, eighth, and tenth minute on the minute the model was raised to the surface and the reaction noted. As a control, every first, third, fifth, seventh, and ninth minute on the minute an observation was made for rises of the tarpon *without* the manipulation of an object. Each observation, control and experimental, at the two minute interval lasted only one second. In general, observations were made during two consecutive hours, or 12 experimental periods each day.

Results. The data in A of Table I indicate that all four types of objects induce imitative rises whose statistical significance compared with the controls is very high. The average rise of a tarpon in the experimental aquarium was twice in ten minutes. In a group of six animals there would be at most twelve seconds of rising in 10 × 60 or 600 seconds; thus, according to the laws of chance, rises of tarpon directly following those of models cannot very well be considered coincidental. It is seen that, of the four objects used, the wooden tarpon model is significantly most effective and the red rubber tubing is second. The degree of success in inducing imitative rises is, however, sharply limited by the physiological state of the animal. As Shlaifer & Breder (1940) demonstrated, a tarpon will not respond imitatively to the rise of another object, even if it be another normal tarpon, unless, by virtue of the fact that the oxygen obtained at the last gulp is distinctly depleted, it is in a "physiologically receptive" state which permits a rising response. The induction of an imitative rise, then, depends on the reaching of a respiratory threshold by the reacting animal. This explains why even the wooden tarpon model enjoys only 48.3% success in inducing rises. The experimental animals may rise either singly or imitatively in groups just before the model is raised to the surface. If so, even raising the object consecutively three times or more will produce no response.

The data in B of Table I demonstrate that objects manipulated so as to rise in an "abnormal" way induce few imitative rises. Comparison with the controls indicates no statistical significance.

Surface Rises in Blinded Tarpon.

That the induction of imitative rises in small tarpon is a visual affair was demonstrated by Shlaifer & Breder (1940). It was found that the rise of a tarpon on one side of a transparent glass plate bisecting an aquarium could induce a rise in others on the opposite side.

Carrying this a step further, four tarpon were blinded by piercing the cornea. Blindness was ascertained by appropriate tests. Several days were allowed for recovery from the operation. Subsequently, the animals were grouped together in 40 liters of standing sea water (oxygen content—2.50 cc. per liter) in a 48-liter aquarium whose dimensions have been listed above.

In the course of several hours of observation no imitative rises occurred. The tarpon rose

Table I.

The Induction of Imitative Surface Rises in Small Tarpon by Various Objects.

A. Object manipulated so as to simulate a normal surface rise.

Type of Model	I Silver Wooden Tarpon	II White Spatula	III Red Rubber Tubing	IV Glass Rod	V Control[2]
Total Number of Attempts[1]	176	181	176	170	703
Number of Successful Attempts	85	52	62	35	12
% of Successful Attempts	48.3	28.7	35.2	20.6	1.7

[1] Object is raised to surface for one second every two minutes in a 10-minute observation period in an attempt to induce a rise in the experimental tarpon in the aquarium.
[2] Observation made for one second every two minutes in the 10-minute period for rises by tarpon *without* manipulation of objects.

Statistical significances (number of successful attempts).*

I vs. II—.0096 I vs. III—.0210 I vs. IV—.0013 II vs. III—.4370
II vs. IV—.2898 III vs. IV—.0210 I, II, III, IV vs. V—.0000

* Upper limit of statistical significance is set at 0.05. This is three times the probable error. 0.01 indicates good significance while a value of 0.100 or more indicates little significance. ("Student," 1925.)

B. Manipulation of object does not simulate a normal rise.†

Type of Model	I Silver Wooden Tarpon	II White Spatula	III Red Rubber Tubing	IV Glass Rod	V Control[2]
Total Number of Attempts[1]	65	65	65	65	260
Number of Successful Attempts	5	5	1	2	6
% of Successful Attempts	7.7	7.7	1.5	3.1	2.3

† Object is raised to surface slowly and parallel with the surface.
[1] See [1] above.
[2] See [2] above.

Statistical significances (number of successful attempts).

I vs. II—None I vs. III—.3342 I vs. IV—.4954 I vs. V—.1832 II vs. V—.2146
II vs. III—.3834 II vs. IV—.4370 III vs. IV—.5580 III vs. V—.5580 IV vs. V—.5580

I (A) vs. I (B)—.0000 II (A) vs. II (B)—.0000 III (A) vs. III (B)—.0000
IV (A) vs. IV (B)—.0000 V (A) vs. V (B)—.4954

individually at the same rate as did the normal animals, once every five minutes. Thus, it is apparent that in the absence of vision no imitative rise will occur; possible response to pressure stimuli does not obtain. The normal rate and type of surface rises in these blinded forms indicates that this pattern of behavior is not dependent on vision for its proper execution though imitative response by one fish to another is.

Locomotor and Respiratory Activity in Waters of Low Oxygen Content.

In previous experiments (Shlaifer & Breder, 1940) it was found that when the oxygen content of the water was increased from 2.50 cc. to 5.60 cc. per liter, the rate of respiratory activity (surface rises) decreased significantly though the locomotor activity remained the same. It becomes desirable, therefore, to determine the respiratory activity and, to a minor extent, the locomotor activity at very low oxygen levels. Small tarpon, incidentally, are relatively hardy forms and are adaptable to a variety of situations. They endure handling in the laboratory remarkably well and would be excellent laboratory material for many lines of research were they to be found more frequently and in greater abundance. They may be found both in the sea and in land-locked pools which are brackish or fresh-water. Some of these pools have relatively little dissolved oxygen but the tarpon survive.

Materials and methods. Tarpon were placed in isolation in 7 liters of standing sea water in 8-liter rectangular battery jars whose dimensions were 20.5 cm. by 18 cm. and 21 cm. deep at the 7-liter mark. The water temperature range was 19–22 degrees C. The rates of surface rises and locomotor activity were determined for 15-minute periods. The rate of locomotor activity was determined by an observational technique which is fully described elsewhere (Shlaifer, 1938). Briefly, 3-cm. squares were ruled in red India ink on all four vertical sides of the rectangular battery jar. Using the eye of the tarpon as an anatomical landmark, the number of squares, actually cubes when projected in space, traversed in a 15-minute period was multiplied by 3 to give the results in centimeters. Since this technique is not as accurate as the simple observation of surface rises and since the experimental vessels, considering the size of the tarpon, were quite small and thus limited activity, the rate of surface rises in this set of experiments may be considered the more important feature. Oxygen content was determined by means of the permanganate modification of the Winkler method.

Results. Comparing the data in Table II with the results of Shlaifer & Breder (1940), it is seen that at the lower oxygen content the rate of respiratory rises increases significantly and the centimeters traversed per rise decreases. The significantly lower rate of locomotor activity at the lower oxygen level may be due primarily to the distinctly smaller vessel in which the tarpon were kept in these experiments rather than to the low oxygen content. As previously mentioned, Shlaifer & Breder (1940) found that while raising the oxygen content from 2.50 to 5.60 cc. per liter in the same aquarium reduced the rate of respiratory rises it did not affect activity. At any rate, the number of surface rises increases at the lower oxygen content despite the decreased activity.

TABLE II.

The Locomotor Activity and Respiratory Rises of Small Tarpon in Waters of Low Oxygen Content.

	Mean Oxygen Content cc./liter	Mean Locomotor Activity[1]	Mean Respiratory Rises[2]	Mean cm. per Rise
A. This set of Experiments	1.02	304.0	3.6	84.4
B. Shlaifer & Breder (1940)[3]	2.40	480.0	2.9	165.5

[1] Expressed in centimeters traversed per fish per 15-minute period of observation. Figure given is the mean of 80 such periods.

[2] Expressed in surface rises per fish per 15-minute period of observation. Figure given is the mean of 80 such periods.

[3] Based on Table I (AI), Shlaifer & Breder (1940). Figures given are for an isolated tarpon in 48 liters of sea water in a 50-liter aquarium. Figures for locomotor activity and respiratory rises represent the mean of 48 15-minute observation periods.

Statistical Significances (A vs. B)
Locomotor Activity: .0003
Respiratory Rises: .007

Finally, it may be noted that if access to the surface is provided, tarpon will survive well in waters of low oxygen content and will utilize relatively more atmospheric oxygen.

SURVIVAL WITH NO ACCESS TO THE SURFACE.

The air-breathing habit in tarpon is peculiar in view of the fact that they normally inhabit fairly highly oxygenated sea water and have rather extensive gill surfaces. The value of the air-breathing habit in land-locked pools of low oxygen content in which tarpon may be found is obvious. However, its persistence in the waters of the open sea may possibly be an indication of imperfectly functioning gills, despite their size. It becomes of interest, therefore, to determine the survival time of tarpon when cut off from access to the surface and thus forced to rely on dissolved oxygen. Hora (1933) states that various air-breathing swamp fishes can be "drowned" if prevented from reaching the water surface. Das (1935) states that the air-breathing loach, *Lepidocephalus guntea*, if prevented from reaching the surface, will be asphyxiated in a little more than an hour. These fishes, however, inhabit waters in which the oxygen content is habitually low in contrast to the tarpon of the open sea.

Materials and Methods. In Expts. 1–7 of Table III, the experimental vessels were 8-liter battery jars whose dimensions have been previously listed. In the first four experiments standing sea water was used; in the fifth, sixth, and seventh, running sea water. In all cases the battery jars were filled to capacity. In the standing water series, a fine wire screen cut so as to insure a tight fit was placed inside the battery jar at the 7-liter mark and in Expts. 5–7 a similarly tight-fitting wooden screen was placed at the same level. In each test the experimental tarpon was allowed a 48-hour period of acclimatization in the battery jar with access to the surface. At the end of that time the screen was put in place and the time and oxygen content noted. Each battery jar contained only one individual at a time. A record was kept of the number of hours between the start of the experimental period and the end, which in every case was at the death of the tarpon. Oxygen determinations were made each day and at the conclusion of the experiment. The locomotor activity and surface rising of the fish were also noted but only in a general way. As controls, individual tarpon were kept in battery jars in running and standing sea water *without* being screened from the surface.

In Expts. 8–13, the experimental vessel was a 56-liter rectangular assembled aquarium with transparent glass sides whose dimensions were 60 cm. by 35 cm. and 27 cm. deep. This was kept constantly filled to capacity with running sea water. The bottom of the aquarium was covered with sand. Into this aquarium was placed a tight-fitting wire mesh screen containing three squares to the inch, at a level of 6 cm. above the bottom sand. The general procedure followed was the same as that described for the battery jar tests except that no observations were made for activity or surface rises.

Results. The data in Table III demonstrate that compelling a tarpon to rely on dissolved oxygen by screening it from the surface will result in asphyxiation in from 7 to 128 hours. Death may occur in a relatively short time even in running sea water (Expt. 5). In the standing water tests the oxygen content at the death of the animal is high enough to maintain a tarpon indefinitely if it is permitted to respire atmospheric oxygen. There seems to be considerable individual variation in survival time. This may be a reflection of individual variations in metabolic rate. In the battery jar tests the tarpon would often make desperate and repeated futile attempts to reach the surface and, failing, would sink exhausted to the bottom, there to remain quiescent for long periods of time. In the aquarium tests, much more area was allowed for normal swimming by the fishes; also, the position of the screen, 6 cm. above the bottom, prevented exhausting and futile attempts to reach the surface. Tarpon in this aquarium, even when not screened from the surface, normally swim near the bottom so that the experimental situation in this case is, except for the screen, quite normal.

In the control tests, tarpon in battery jars with access to the surface survived indefinitely even when the standing water oxygen content was quite low.

Discussion.

It is interesting to note in the model experiments that imitative rises may be induced by very crude objects differing appreciably in form and color. At the same time, a more finished wooden model is more successful than are the crude ones. The results in B of Table I indicate that movement rather form or color is the important factor for, if the model is so manipulated that the normal rise of a tarpon is not simulated, there is no significant induced imitation, even with the wooden model. Nevertheless, a properly manipulated silver wooden model is more successful than are properly manipulated objects that are distinctly cruder models. Apparently, then, form and/or color may also be involved but only in a minor supplementary way. Possibly at a distance of several inches or more from the reacting tarpon the type of wooden model used was more visible than were the other objects. Using this imitative rising reaction, it may be possible, by employing a great variety of objects differing in form and color but manipulated normally, to obtain data which may be of significance in obtaining a measure of the visual acuity of tarpon. The data already obtained, showing as they do only a slight though real difference between a good and a crude model in their relative success at inducing rises, tend to indicate that such experiments would require considerable data to have any significance.

Table III.

Effect of Prevention of Surface Rises on the Survival of Small Tarpon.

Experiment No.	Water	Oxygen Content*	Survival in Hours	Remarks
1[1]	Standing	3.39-2.20-1.60	53	Periods of great activity and attempts to reach surface followed by periods of quiescence.
2[1]	Standing	3.47-2.98-2.70-2.52	71	"
3[1]	Standing	4.15-3.20-1.68	51	"
4[1]	Standing	4.07-1.92	11	Tarpon very active—many attempts to reach surface.
5[1]	Running	4.86	7	Tarpon very active.
6[1]	Running	5.58	72	Activity and rises of fish increase markedly one day before death.
7[1]	Running	5.58	128	
8[2]	Running	5.58	32	
9[2]	Running	5.58	115	
10[2]	Running	5.58	125	
11[2]	Running	5.58	24	
12[2]	Running	5.58	34	
13[2]	Running	5.58	46	

* In the standing water experiments, the oxygen content is given day by day in cc. per liter. The final figure represents the oxygen content of the medium at the death of the experimental animal. In the running water series, the figures given represent the average oxygen content in cc. per liter day by day.
[1] Experimental vessel is an 8-liter battery jar.
[2] Experimental vessel is a 56-liter aquarium.

In several cases attempts were made to revive tarpon which, after a long period of time, were near asphyxiation and lay on their sides. They were permitted to come in contact with the surface but evidently were too far gone, for they soon died. In one case, however, three blinded tarpon, which when screened from the surface in standing water in a battery jar soon approached exhaustion and asphyxiation, did recover when the screen was removed after one hour. In that time, unlike normal tarpon, they kept rising almost continually in attempts to penetrate a screen which they could feel but could not see and within 40 minutes lay on their sides. Das (1935) reports that the air-breathing loach will recover from partial asphyxiation if permitted to rise to the surface after being kept under a screen.

It has been seen that preventing a tarpon from utilizing atmospheric oxygen will eventually be fatal, even in highly oxygenated water. Hence, there is no question of the survival value of the surface rise pattern of behavior in these forms. In contrast to the work of Hora (1933) and Das

(1935), the asphyxiation of tarpon under screens is a very slow process. Undoubtedly there is interesting material here for exhaustive physiological studies.

It is quite difficult to evaluate the pattern of imitation in surface rising in a group of tarpon. Shlaifer & Breder (1940) have shown that imitation will not occur, apparently, until a respiratory threshold is reached. An isolated tarpon will rise periodically in response to physiological need and over a period of time not much more frequently if it is in a group. It is difficult, at least at this time, to attribute any adaptive value to this imitative behavior which might be termed "social respiratory facilitation."

Summary.

1. Imitative air-gulping surface rises in small tarpon may be induced by relatively crude models if they are manipulated so as to simulate the normal surface rise of this form. A relatively more life-like wooden tarpon model is more successful than are the cruder objects. No significant success is attained with any model if its manipulated rise differs appreciably from the normal.

2. The imitative pattern is based on visual stimuli rather than on differential pressure stimuli. Blinded tarpon never rise imitatively.

3. At distinctly low oxygen levels, the rate of respiratory rises increases but if access to the surface and hence to atmospheric oxygen is maintained the tarpon survive.

4. Tarpon when prevented from utilizing atmospheric oxygen succumb in 7 to 128 hours even in highly oxygenated running sea water.

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